planted by John Hall east of Alvarado in 1865 are still standing. The grove of blue gums on the University of California campus, Berkeley, was planted shortly after 1870 and some of these trees are now over 170 feet in height. The date is based upon statements made to the writer by a daughter of Rev. Samuel H. Willey who lived in Berkeley up to 1870, and by Joseph Rowell, archivist of the University, who has lived continuously in Berkeley since September, 1873. Pictures in possession of the writer further confirm the general age of the campus trees. A large manna gum on the campus at Berkeley is 64 inches in diameter, breast high. Several other trees of notable size could be included in this list, but all these belong to a later day. People who have unusual specimens of eucalyptus to report or who have additional facts concerning the early history of the eucalyptus in California are invited to get in touch with the writer or the Extension Forester, College of Agriculture, University of California, Berkeley.

The eucalyptus is now one of the outstanding trees on almost any California landscape where trees have been planted. Many people fail to realize that this tree is not a native. At this late date we can pay our respects to the early pioneers, such as William C. Walker and Stephen Nolan, and hope that some of our present generation also will be inspired to become pioneers in the introduction of worthy exotic trees to supplement our rich native flora.

College of Agriculture, University of California,
August, 1935.

ON THE GENUS PITYOPUS

Herbert F. Copeland

The genus *Pityopus* has been something of a mystery. The name seems to mean "pine foot." Published by Small twenty years ago, the original description could be overlooked by no student of the saprophytic plants which make up the monotropoid alliance: but there have heretofore been no additions to our knowledge of the plant, nor even any reports of new collections. A single species, *P. oregona,* was described. It was suggested that a plant collected by Eastwood and described by her as *Monotropa californica* might represent the same species. But meanwhile Domin reduced Eastwood's plant (of which he could have seen no material) to a variety of *Monotropa Hypopitys.*

My studies, pursued with much deeply appreciated assistance (more detailed acknowledgements are made below), enable me to list six collections. The suggestion that *Monotropa californica* is identical with *Pityopus oregona* is confirmed. The long aban-

doned "Rule of Kew" would have spared me the formal necessity of giving this species a third name. Publication of the following involves responsibility; no "credit" is available.

Pityopus californica (Eastw.) Copel. f. comb. nov. *Monotropa californica* Eastwood, Bull. Torr. Bot. Club 29: 75–76, pl. 7, figs. 1–9. 1902. *Pityopus oregona* Small, North American Flora 29: 16. 1914. *Monotropa Hypopitys* var. *californica* Domin, Sitzber. böhm. Ges. Wiss. II Classe, I Stück p. 24. 1915.

Known collections: Oregon. North of Mount Hood, *Thomas Howell,* July 3, 1891 (Herb. N. Y. Bot. Gard.); Curry County, Rogue River between Lowery's and Agness, *L. F. Henderson,* July 6, 1929 (Herb. Univ. Oregon); Lane County, Westlake, *Mrs. Lucina Richardson,* May 18, 1928 (Herb. Univ. Oregon). California. Hupa Indian Reserve, 1000 ft., *Harley P. Chandler,* June, 1901 (Herb. Univ. Calif.); Marin County, Little Carson Creek, *Alice Eastwood,* May–June, 1901 (Herb. Calif. Acad. Sci.); Fresno County, Sequoia Lake, 5500 ft., *George H. Quick,* July, 1934 (Herb. Univ. Calif.).

For the opportunity to examine Quick's specimen and for other favors, I am indebted to Dr. H. L. Mason. Examination of this specimen was the occasion for the present study; fragments from it were the material for the anatomical work reported below; all the drawings except figure 3 of Plate V were made from it. It consists of the upper part of a single shoot preserved in alcohol.

My inquiries after Howell's specimen at the New York Botanical Garden were courteously answered by Dr. Small and Dr. Gleason; but these gentlemen and I were disappointed by the discovery that the specimen had disappeared.

Miss Eastwood made two collections of the plant at the same locality. A single very immature shoot, collected May 30, 1901, survives as a dried specimen. The more important collection made a week later, the basis of the description and illustration of *Monotropa californica,* was preserved in alcohol and was lost in the disaster of April, 1906. The collector's subsequent careful searches in the field have revealed no more of the plant. The situation of *Pityopus californica* is unusual; the type specimens of the genus and of the only species were distinct, and both are lost. I was permitted to dissect a scrap which had been taken from Eastwood's surviving specimen and given to the University of California. It was so very scant and immature that I tried imbedding it in paraffin and sectioning with a microtome. The result is a lot of sadly shattered sections (imbedding in collodion might have yielded better results); nevertheless, the crucial question as to whether the placentation is parietal or not is answered in the affirmative.

Chandler's specimen, consisting of the upper parts of two shoots, collected by coincidence the same month as Eastwood's

lost material, had lain all these years in the Herbarium of the University of California with a doubtful identification as *Monotropa fimbriata.*

The inadequacy of the material already mentioned is obvious. Hoping against hope for a chance to see better material, I wrote to the University of Oregon. Mr. L. F. Henderson, the veteran botanist of that institution, had the kindness to lend two very abundant and excellent specimens. These have fully satisfied me as to the identity of the other collections.

Gross Morphology

Pityopus shows many of the characters of *Hypopitys;* specimens of the rare genus are likely to be misidentified as representing the commoner one. The essential difference is in the placentation, which is in *Pityopus* parietal, in *Hypopitys* axile. There are other, more readily observed, differences. Shoots of *Pityopus* are strictly erect, and when in full flower are said to be white (except the yellow stigma and pink anthers). Presumably they darken with age; dried and preserved specimens are intensely black. Excepting the interior of the flower, the plants are essentially glabrous. They are often distinguishable from *Hypopitys* by greater size; stems commonly exceed 1 cm. in diameter; the perianth is usually over 1 cm. long. Henderson's collection shows intergrades between the ordinary stout and massive type and such diminutive individuals as Eastwood's surviving specimen.

Whole plants are approximately 7 to 20 cm. tall. Roots have been seen only on Mrs. Richardson's collection; they are like those of related plants, forming small globular clusters at the bases of the shoots.

The shoot consists of a scaly stalk bearing a bracteate inflorescence. The largest foliar organs are the highest "leaves" and lowest "bracts" at the transition from "stem" to "rachis"; these may be 2 cm. long; the lower "leaves" and higher "bracts" are smaller. "Leaves" are generally ovate, entire, rounded, attached by the broad base; "bracts," especially the upper ones, are narrowed below (*i.e.,* cuneate as to base), erose as to margin, more or less acute.

Domin (3) has devoted several pages to elucidating the great variety of inflorescence observed in *Hypopitys.* He treats all the races of this group as varieties of *Monotropa Hypopitys.* The inflorescence of *Pityopus* is similarly variable; but without an extensive set of preserved collections (as distinguished from dried specimens) it is not possible to describe it in detail. Sometimes (*cf.* Eastwood's fig. 1) there is a terminal flower which opens before the others. On the other hand, Quick's specimen appeared to show a typical raceme, the flowers opening in acropetal succession and the summit of the rachis occupied by an ordinary

terminal bud, a body of rudimentary bracts and flowers. In this raceme, each flower is terminal on an axillary pedicel which is stout and naked; the lowest pedicels are about 1 cm. long. In Henderson's collection and in Mrs. Richardson's, another variation appears. The axillary structures are not the pedicels of single flowers, but are cymelets each consisting of a short secondary axis bearing bracts, axillary flowers, and a terminal flower which opens first.

The flowers may be pentamerous or tetramerous. In Eastwood's figure the terminal flower is pentamerous. This is the condition of the flowers of Mrs. Richardson's collection; in Henderson's the flowers are tetramerous. In both collections the terminal and axillary flowers seem to be alike, pentamerous or tetramerous as the case may be. The flower of Quick's collection (pl. V, fig. 1) are tetramerous.

Small described the sepals as four or five in number. Ideally, no doubt, they are as many as the petals; actually they are often fewer. On Mrs. Richardson's specimen, most flowers of which have five petals, Henderson noted "Calyx-bracts generally 2, often 4." Two flowers of Quick's specimen showed respectively a whorl of three (the abaxial sepal, sheltered by the bract, being suppressed) and a whorl of three with a fourth inserted at a higher level, among the petals. These sepals in fully developed flowers are 1 cm. long or a little more (about 2 cm. long in an apparently monstrous flower of Chandler's collection); they are glabrous, elliptic to obovate, ordinarily acute, erose.

The petals are slightly longer than the sepals. They are slightly but definitely saccate at the base, commonly obovate, acute, erose, glabrous without and densely pubescent within.

Of stamens I have consistently found twice as many as the petals. They are variable in length, usually slightly (sometimes considerably) shorter than the pistil. The slender filaments are densely pubescent above. I have not seen anthers before dehiscence. All the anthers seen had doubtless been more or less globular (cf. Eastwood's figs. 6–9). They can be described as usually opening by a single valve on the outer or dorsal side (pl. V, fig. 2; cf. Eastwood's fig. 9). In two individuals of Henderson's collection, the valve has consistently failed to become free at the summit, and the anthers may be said to open through widely gaping pores (pl. V, fig. 3). It is hard to harmonize these observations with the original description, "each sac opening by a short slit on the side." Possibly that was based on young anthers of which the pores would later have gaped widely.

The nectary consists of a belt around the base of the ovary, and, borne upon it, a whorl of mamilliform projections. These projections are arranged in pairs opposite the petals and embracing the bases of alternate stamens. They are less prominent than the similarly placed projections of *Hypopitys,* as described

by Oliver, and very much less prominent than the rod-shaped projections of *Monotropa uniflora.*

The pistil (pl. V, fig. 4) is about as long as the perianth. The upper part of the ovary and the style are pubescent; there is a conspicuous collar of hairs just below the stigma, as in *Monotropa, Hypopitys,* and *Newberrya.* The superior ovary is globular, up to 7 mm. in diameter or even larger in some flowers of Chandler's collection. The style is about as long as the ovary; the stigma is capitate. This character is not well brought out in Eastwood's figure 5, but is evident in the surviving specimen of her collection.

There is, on the upper surface of the stigma, a deep depression which is actually an opening into the fluted style-channel. The latter leads to the interior of the ovary, which is almost filled by several placentae. These placentae are essentially of the same structure as in *Newberrya,* but are massive rather than trilamellate, appearing ovate or lanceolate rather than hastate in cross section. They are connected to the walls of the ovary by bands of tissue which appear in cross section as narrow isthmuses. The normal number of placentae is apparently twice the number of petals; actually, in three ovaries of Quick's specimen there were respectively seven, nine, and eight (of which two were partially coalescent). Henderson noted six or seven in Mrs. Richardson's collection. In Chandler's collection there are more than five, but the exact number could not be determined in the dried material. In the shattered sections of the ovary from Eastwood's collection, several internal masses were recognized as placentae by the presence of vascular tissue (this would be absent from the septa of a plurilocular ovary); but the number could not be determined.

Anatomy

From Quick's specimen were removed a length of stem, two whole flowers, and fragments of two others. These objects were transferred through the series of mixtures recommended by Zirkle (15) to butyl alcohol; imbedded; and sectioned. Both cross and longitudinal sections were made from the stem. From the two whole flowers, serial cross sections, respectively at 15 and 20 microns, were cut. The fragments of flowers furnished longitudinal sections of the pistil. The sections were mounted and stained in various fashions, mostly with safranin and light green. Some were cleared in xylol and mounted in balsam without staining; the black pigment present in the material made it possible to see many details. Preservation in alcohol was found to have fixed the material satisfactorily for most purposes; only the ovules were decidedly unsatisfactory. Incidentally, the series of mixtures of ethyl and butyl alcohols recommended by Zirkle for dehydrating fixed objects was found equally satisfactory for hydrating and dehydrating mounted sections in the process of

staining. The different series of mixtures which Zirkle (16) has more recently suggested for use in the latter process is unnecessary for ordinary anatomical purposes.

In the course of describing this material, I shall have occasion to compare *Pityopus* with related plants. For comparison I have several sets of serial sections of *Pterospora* and *Sarcodes;* a few of *Newberrya,* already described (2); and an abundance of material of *Pleuricospora.* I look forward to preparing an account of the morphology of this last genus, but it is harder to do justice to unlimited material than to such scraps as I have had of *Newberrya* and *Pityopus.* Much work on *Hypopitys* has been published in Europe; I have not had access to all of it, but the older papers are summarized by Drude (4). The account of *Sarcodes* by Oliver (10) is well known. The ovules of the group are described by Koch (9), Samuelson (11), and Schnarf (12). I may also cite my own recent publications (1, 2).

The roots of monotropoid plants are known to show peculiarities. In *Hypopitys* the branch roots originate in normal fashion, that is, internally. In *Sarcodes* and *Pterospora,* Oliver made the interesting discovery that branch roots arise exogenously; and I have found that the same thing is true in *Pleuricospora.* Some authors[1] have concluded that the monotropoid plants possess no true roots, but instead an organ *sui generis* to be called the procaulon. For the discussion of this interesting problem it is not yet possible to draw any data from *Pityopus.*

The stem shows in cross section (pl. V, fig. 5) an epidermis, a cortex, a vascular cylinder, and a large pith. Pith and cortex alike consist of large cells elongated parallel to the axis of the stem. The walls are thin and show abundant thinner places or large and very shallow pits. The cells of the epidermis are somewhat smaller than those of the cortex. There is a thin cuticle; it shows obscurely a tendency toward the ridged condition which is more conspicuous on the floral organs.

The vascular cylinder is of a small but varying number of layers of cells. The cells are mostly slender, elongate, thin-walled, and nucleate. Cells recognizable by lignified walls are remarkably scarce. They occur in scattered patches on the inner side of the vascular cylinder (indicated in figure 5 [pl. V] by little specks of solid black). The arrangement of these patches is definite to the extent that they are absent from the leaf traces; possibly with more abundant material other regularity could be made out. The lignified elements are spiral or scalariform. The cylinder as a whole is star-shaped. The angles are directed toward leaf-attachments; leaf traces, each consisting of a single strand and leaving a single gap, are recog-

[1] Domin (3, pp. 47–49) accepts this view and cites several works of Velenovsky, especially his Vergleichende Morphologie der Pflanzen Bd. II (1907) p. 367.

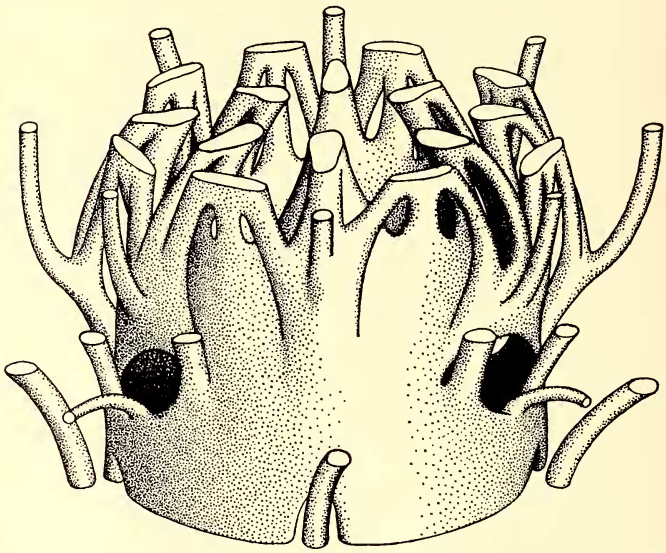

Fig. 1. Reconstruction of the vascular system in the receptacle, approximately × 25.

nizable. This structure is essentially identical with that of *Newberrya* and *Pleuricospora*. In *Pleuricospora* there are, in the stem proper, no axillary bud- or branch-traces; in the axis of the inflorescence, each flower trace consists, as one would expect, of two conspicuous bundles, one on each side of the bundle which runs to the subtending bract. It is assumed that the structure is the same in *Pityopus*.

In the pedicel the vascular tissue forms a cylinder. Near the receptacle the sepal traces become separated by rays of ground tissue from the rest of the cylinder. The small gaps left by the departure of the sepal traces are closed at a slightly higher level. Deviations from the normal arrangement of the sepals are reflected in the vascular anatomy. Of the two flowers from which my sections were made, one, lacking a sepal on the abaxial side, shows no vestige of a sepal trace on that side; the other (pl. VI, figs. 1–4), in which one sepal is inserted at a higher level than the others, has the bundle supplying it at about the same level as the petal traces.

The vascular supply to each petal consists of three bundles; the median bundle, which bends downward to pass under the nectar sac of the petal, is smaller than the laterals, which pursue an upward course from the beginning. The departure of the three bundles to each petal leaves a single large gap which closes quickly. No very significant irregularities were observed in this

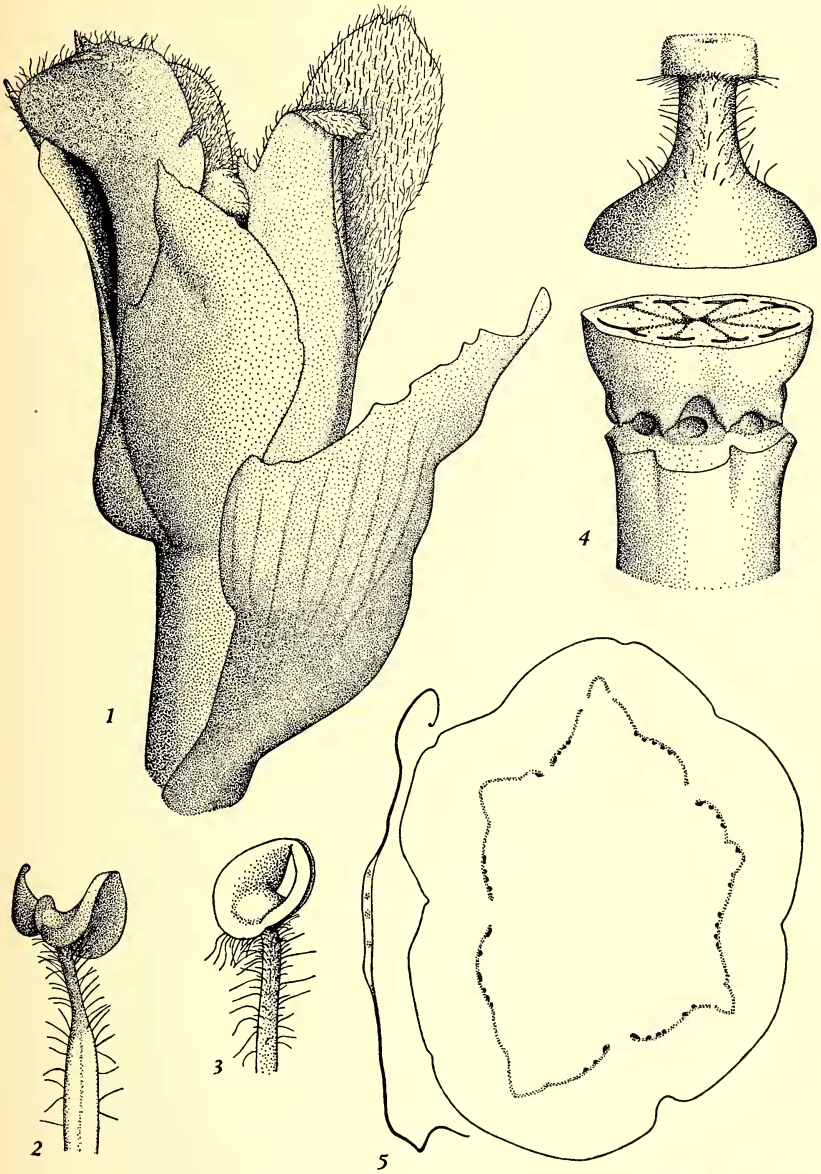

PLATE V. Fig. 1. Flower × 5. Fig. 2. Anther × 10. Fig. 3. Anther from Henderson's collection × 10. Fig. 4. Sectioned pistil × 5. Fig. 5. Cross section of the stem × 5.

whorl: one of the laterals may arise from the side of the median bundle, or vice versa.

The structure of the vascular system above the insertion of the petals varies to some extent from sector to sector (pl. VI, figs. 3, 4; pl. VII, figs. 1–3). It is possible to figure out what the arrangement would be if all the bundles were fully developed (text fig. 1); the result is not easily interpreted in terms of the commonly accepted theory of receptacular vascular anatomy as it has been expounded by Eames and others (5, 6 pp. 279–284, 7, 8, 13, 14).

From the vascular cylinder depart eight large bundles, leaving small gaps. One of these bundles is directed toward the base of each stamen. The ones which lie in the radii of the petals arise at a slightly lower level than those opposite the sepals. This arrangement is related to the existence of a pair of the mamilliform projections of the nectary opposite each petal, and to the consequent somewhat lower insertion of the stamens between them; it is not taken as an indication that the stamens form more than one whorl. The bundles just mentioned are not simply stamen traces. They fork periclinally, and only the outer and much smaller branches run in a radial direction into the bases of the filaments. The larger, inner branches proceed upward into the base of the ovary, toward the inside from the glandular tissue of the nectary. For purposes of definite reference, I may call these the supernumerary bundles. They may presently fade out; but usually, either without branching or after forking into two or three parts, they become part of the vascular system of the pistil.

Above the departure of the bundles just described, the vascular cylinder breaks up into an indefinite number of separate bundles. The bundles lying more or less in the radii of the stamens pass into the placentae. The supply to each placenta seems often to consist of two or more bundles, and may be regarded as representing the paired ventral bundles of adjacent carpels. The bundles which do not pass into the placentae become carpel dorsal bundles and proceed up the wall of the ovary, one of them in each space between the attachments of two placentae.

If, in the base of an ovary, a "supernumerary" bundle has divided into three branches, then the middle branch, lying in the radius of a stamen and a placenta, bends inward and increases the vascular tissue of the placenta; while the two lateral branches diverge and finally become fused with the adjacent carpel-dorsals. If a "supernumerary" bundle fades out or fails to divide into three parts, then one or more of the connections just described remains unmade.

The difficulty of interpretation mentioned above lies in the "supernumerary" bundles. These are constantly present, fused

PLATE VI. Figs. 1–4. Cross sections of pedicel, receptacle, and flower × 10. The interval between figs. 1 and 2 is 0.5 mm; between 2 and 3, 0.3 mm; between 3 and 4, 0.35 mm. Vascular tissue stippled; nectary cross-hatched.

to the ventral side of the stamen traces; they enter the pistil along the radii of the placentae, that is, in positions alternating with the theoretical positions of the carpels; and typically, as I take it, they fork trichotomously. One possible interpretation is that these are the valid pairs of fused carpel-ventral bundles from adjacent carpels; this may be the true interpretation in spite of the fact that branches run back from them to the carpel-dorsals, and that they do not constitute the main vascular supply to the placentae. Another interpretation would make the "supernumeraries" represent an outer whorl of carpels, alternate with and completely adnate to the proper carpels, and so completely suppressed as to be recognizable in no feature except these bundles. It is a peculiar fact that in *Newberrya* and *Pityopus* (not *Pleuricospora*) parietal placentation is associated with a double number of carpels. It is conceivable rather than probable that in *Pityopus* the number is actually quadrupled. A third interpretation takes into account the conception, that when carpels are organized as a compound pistil, the new organ is capable of modifications not referable to the carpels which are its elementary components; and recognizes the "supernumerary" bundles as structures *sui generis*. My observations suggest no choice among these possibilities. Possibly studies of *Hypopitys* and *Monotropa* may be helpful; nothing pertinent was noticed in *Newberrya*.

Lignified conducting cells are few in the flower as in the stem; the vascular tissue consists mostly of thin-walled elongate living cells. No peculiarities of the ground tissue were noted. The epidermis of sepals, petals, filaments, and style, and of the upper part of the style channel, bears a cuticle which is externally ridged; the ridges are minute (several to the cell) and sharp, and run parallel to the axis of the flower. The epidermis of the nectary and pistil is notably dark-staining. The small cells which make the nectary also stain darkly, but in a different fashion, showing less affinity for safranin than the epidermis and more for light green.

The hairs, which are abundant on the inner surface of the petals, on the filaments, and on the upper part of the pistil, and which are especially long and stout just below the stigmatic surface, are altogether similar to those of *Newberrya;* they are extensions of epidermal cells, lack cross walls, stain darkly, and are covered with a cuticle which is minutely longitudinally ridged. Within the style channel the cuticulate epidermis gives way to an epidermis of appressed, dark-staining cells without cuticle; this covers the placentae and inner surface of the ovary wall.

The anther walls consist of a single layer of cells, thick-walled, and wrinkled in dehiscence, but without rib-like thickenings. This layer is evidently an exothecium. Normal fully de-

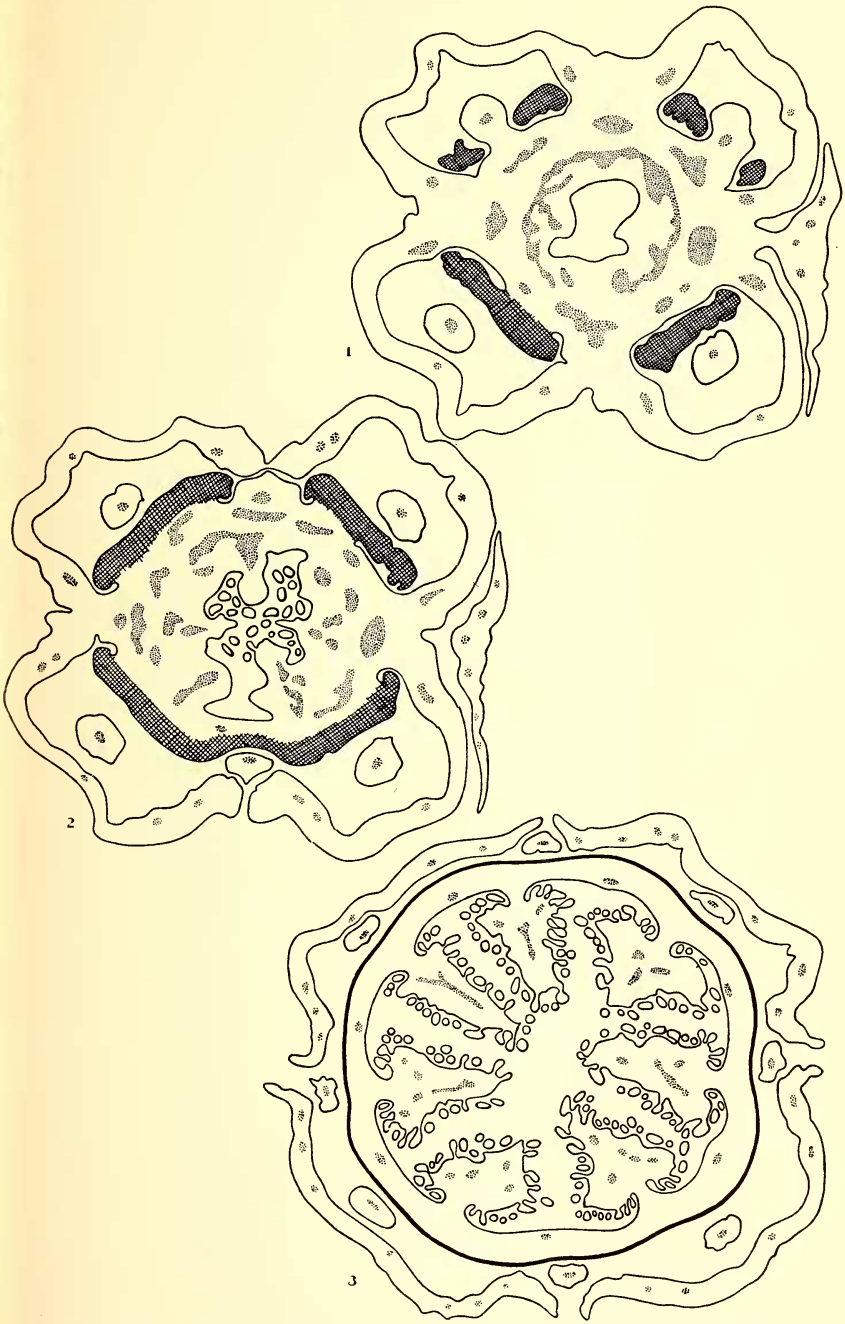

PLATE VII. Figs. 1–3. Cross sections of pedicel, receptacle, and flower × 10. The interval between pl. VI, fig. 4, and pl. VII, fig. 1 is 0.2 mm; between 1 and 2, 0.2 mm; between 2 and 3, 2.2 mm. Vascular tissue stippled; nectary cross-hatched. Sepals are omitted in figs. 1–3.

veloped pollen grains were not seen. The grains as seen on the stigma are solitary (not in tetrads), and smooth walled; they show germination through two opposite pores.

The ground tissue of the style consists of elongate cells compactly arranged in more or less definite rows. As these rows extend into the stigma, the cells become broader and shorter and show a tendency to stain darkly. The stigmatic surface consists of a single layer of finger-shaped cells, darkly staining and lacking cuticle, which stand out separately from one another. Figure 1 (pl. VIII) would appear to show more than one layer of such cells; this appearance results from slightly oblique sectioning. This stigma is histologically quite similar to those of *Sarcodes, Pterospora, Pleuricospora,* and *Newberrya.*

The stout hairs just below the stigma seem to act as a basket for accumulating pollen grains, and may be of some effect in preventing self-pollination, as the anthers in the same flower do not extend above them. Pollen tubes, faintly stained, can be followed from the pollen grains in among the finger-shaped cells of the stigmatic surface, but not definitely any farther. Certain elongate darkly staining bodies seen among the cells of the style may or may not be their advancing tips.

The ovules in my material (pl. VIII, figs. 2, 3) are poorly fixed and are all in a brief range of stages from just before to just after fertilization. They show perfectly standard stages of erical embryology. The ovule has an integument of about two layers of cells; the nucellus has been absorbed and the embryo sac is of the normal type. Figure 2 (pl. VIII) appears to show the penetration of a pollen tube: the two synergids have become flattened against the inner surface of the integument; the pollen tube extends between them and beyond them, within the egg cell, toward the egg nucleus. Figure 3 (pl. VIII) shows the two-celled endosperm; the four-celled endosperm has also been seen.

Discussion and Conclusions

Pityopus is, of all plants known, the one most closely related to *Hypopitys;* the relationship between the two groups is even closer than that between *Hypopitys* and *Monotropa uniflora.* The genus *Newberrya* stands not far from those already mentioned; *Pleuricospora* is more distant. Placentation may be a useful character in constructing keys to the genera of monotropoid plants; it is not usable in gathering these genera into natural groups.

The anatomical peculiarity of the receptacle (describable as consisting of the intercalation of a whorl of bundles, to which the staminal bundles are adnate and which lie outside of the proper pistillar bundles) is of no great theoretical significance.

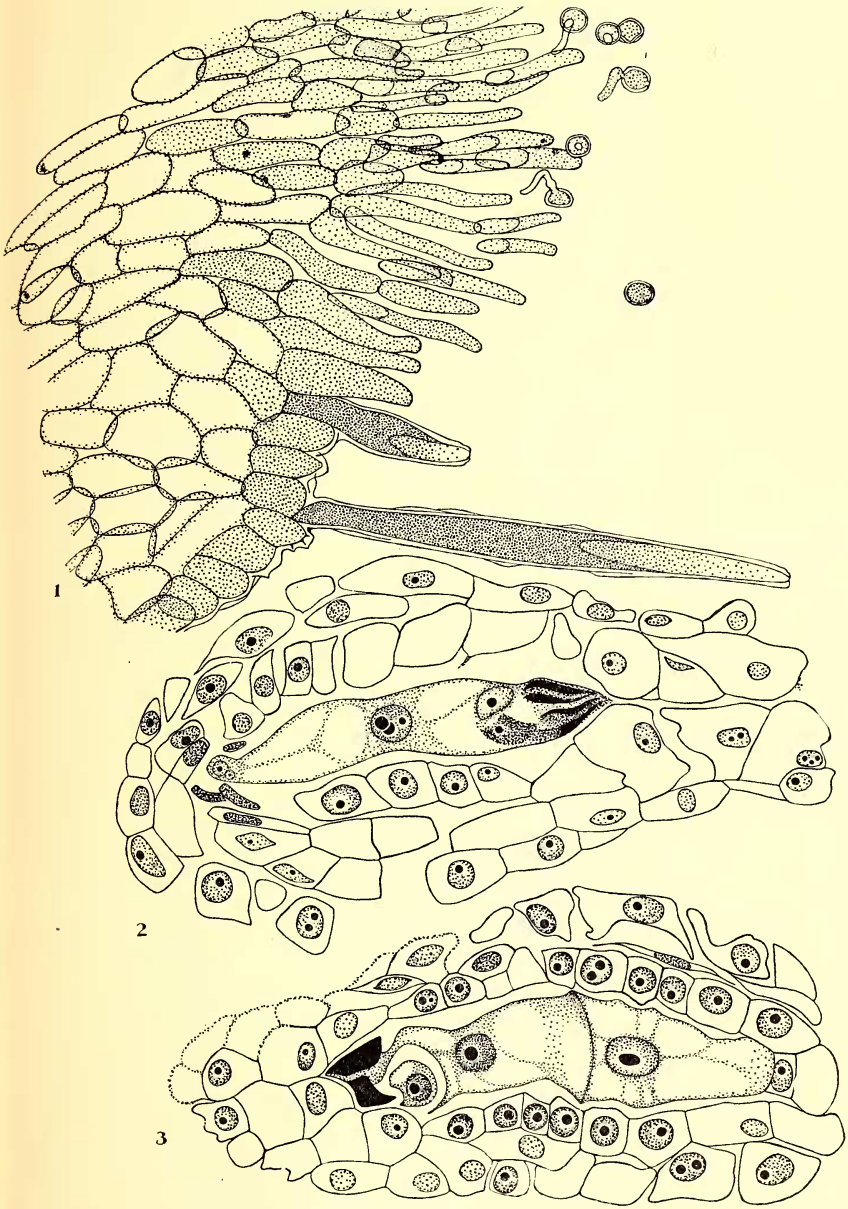

PLATE VIII. Fig. 1. Longitudinal section of the edge of the stigma × 200. Fig. 2. Ovule showing fertilization (?) × 400. Fig. 3. Ovule showing two-celled endosperm × 400.

This character is almost certainly not primitive, but something which has appeared in a small derived group.

While consistently treating *Pityopus* as a proper taxonomic group, I have been struck with the possibility that it is not. This uncertainty rests on the following combination of facts: the plant differs from *Hypopitys* in only one essential character, namely, parietal placentation; the two specimens most carefully studied—those of Quick and of Mrs. Richardson—are definitely not alike in inflorescence and number of placentae; the occurrence of the plant is sporadic, and confined to a region where other monotropoid plants are not uncommon. Quick collected it in association with *Pleuricospora,* and Mrs. Richardson, as Henderson noted, "with *Hypopitys, Allotropa,* and later with *Newberrya.*" These facts are consistent with the possibilities, either that *Pityopus* is a repeatedly appearing mutant of *Hypopitys* or else that it is a hybrid. For the present, *Pityopus* is to be regarded as a valid genus; but more data are desirable.

Sacramento Junior College,
Sacramento, California,
March, 1935.

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